A New and Unique, Mat-forming Merlin's-grass (Isoëtes) from Georgia

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The quillworts, *Isoëtes* (Lycopsida, Isoëtales), constitute a heterosporous family of about 60 species recognized by botanists since the time of Linnaeus as having fleshy, two-, three- or four-lobed corms with a crown of spirally arranged, ligulate microphylls and numerous dichotomizing roots that emerge in series along the median furrow(s) of the corm.

Vertical stem growth in *Isoëtes* results from a shoot apical meristem that produces sterile and fertile leaves and a central core of primary vascular tissue. Expansion growth is effected by the activity of a lateral meristem or "cambium" that encloses the primary vascular cylinder. During growth in girth, the original corm structure is maintained by radial displacement and seasonal loss of the outer, older leaves, roots, and corm tissue.

Sexual reproduction involves the formation of micro- and megasporangia, the spores of which develop endosporically into male and female gametophytes. Water-mediated cross fertilization produces daughter sporophytes.

Developmentally, young sporophytes exhibit a distinct change in their overall morphology (Paolillo, 1963). During the first 10-15 plastochrons, leaves are produced alternately on either side of the embryonic shoot apex. During this stage, the apical meristem produces neither cauline vascular tissue nor primary stem growth; thus the vasculature of these distichous juveniles consists of a sympodium of traces to leaves and roots on either side of the shoot apex and median furrow. The resultant two-ranked leaf arrangement is lost, however, as soon as the apical meristem becomes large enough to initiate leaf primordia in a spiral sequence. Apparently, this apical enlargement also is responsible for the differentiation of the vascular core and the concomitant inception of vertical stem growth.

Vegetative propagation is rare in *Isoëtes*. Goebel (1879) reported it in *I. echinospora* Dur. Goebel (1905, p. 431) also reported adventitious plantlets on *I. lacustris* leaves in a sporangial or sub-sporangial position in sterile specimens from the Vosges Mountains of France. Similar sterile but viviparous plants of *I. lacustris* were reported from Windmere, England by Manton (1950, p. 255). The developmental origin of such epiphyllous plantlets is not understood and is in need of investigation.

Branching in the upper portions of *Isoëtes* axes, another mechanism of vegetative reproduction, also has been reported (Motelay & Vendryes, 1882; Solms-Laubach, 1902; Eames, 1936, p. 51), and a recent developmental study has revealed basal branching in two species of *Isoëtes* (Karfalt & Eggert, 1977).

With the exception of branching and bud-formation, the quillworts traditionally have been considered as a morphologically uniform family of pteridophytes. The discovery of the Peruvian genus *Stylites* (Amstutz, 1957), however, has expanded

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our biological and morphological concept of the Isoëtaceae. Detailed developmental and morphological studies of *Isoëtes* (e.g. Paolillo, 1963), *Stylites* (Rauh & Falk, 1959 a, b), and the structural intermediate of these two genera, *I. triquetra* A. Br. (Kubitzki & Borchert, 1964), have indicated that the family Isoëtaceae actually represents a polymorphic, clinal complex probably best treated as a single genus.

The profound influence of microhabitat upon *Isoëtes* morphology (Kubitzki & Borchert, 1964; Matthews & Murdy, 1969) must be considered in order to understand the complex polymorphism encountered within this family. The recent recognition of the following new and unique species of *Isoëtes* that is a narrow endemic in the Piedmont of Georgia further emphasizes the influence of habitat upon *Isoëtes* morphology and supports the concept of the extant Isoëtaceae as a polymorphic, monogeneric family of pteridophytes.

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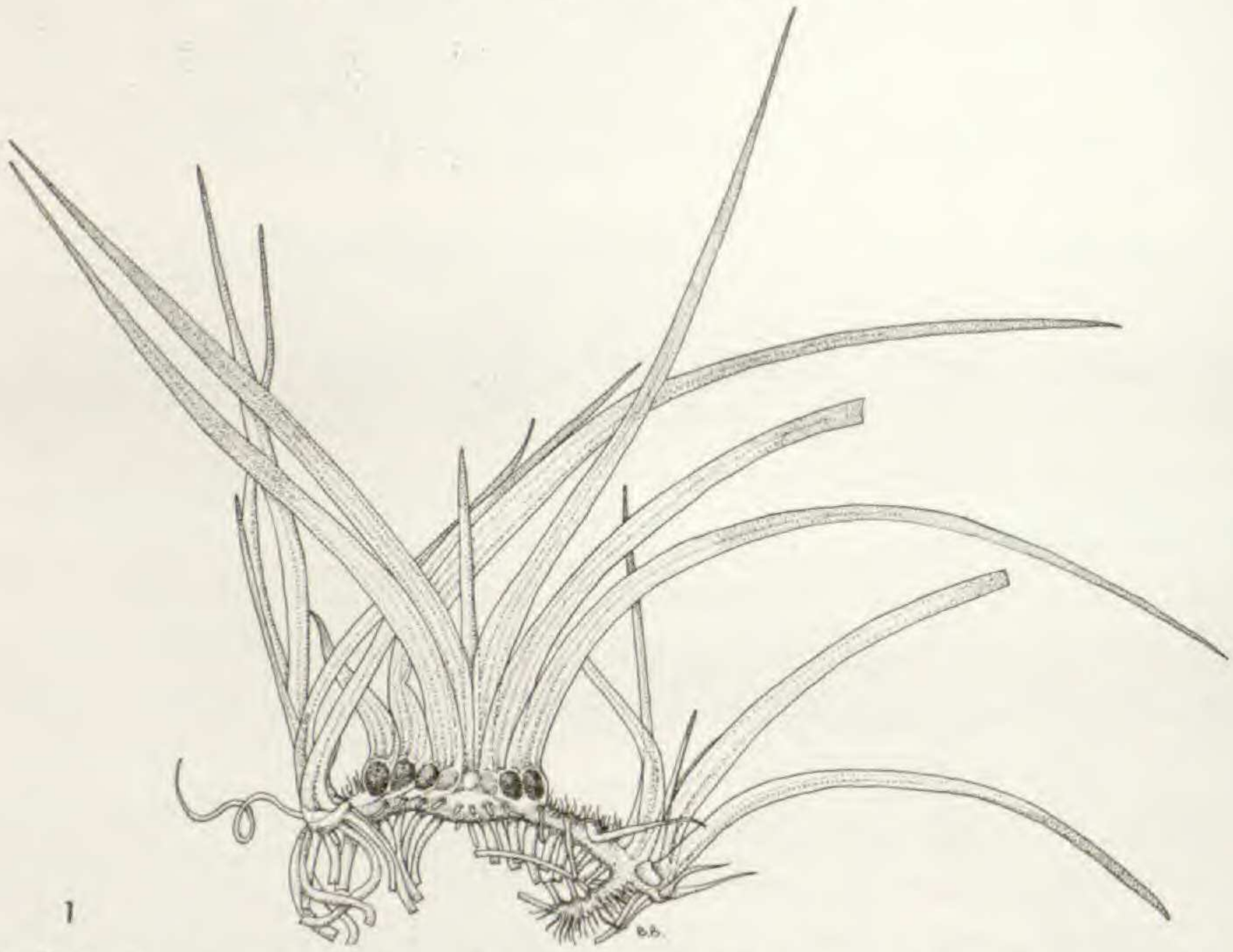


FIG. 1. Habit of *Isoëtes tegetiformans*. Triple plant with roots trimmed exhibiting seven microsporangia and distal, adventitious plantlets, × 3. [Drawing courtesy of Ms. Betsy Birkner, Staff Artist, Dept. of Botany, U.N.C., Chapel Hill]

Isoëtes tegetiformans Rury, sp. nov. **Figs. 1-8.**

Plantae amphibiae, sine cormis, tegetes formantes, plantulas distales adventitias saepe gerentes. Caulis prostratus, centraliter sulcatus, 3-35 mm longus, 0.5-1.5 mm diam., saepe deorsum tortus vel curvatus; radices non dichotome furcatae, plerumque in seriebus tribus linearibus secus sulcum medium utrinque dispositae: radices duae graciles laterales et una crassa (saepe spiralis) basalis una cum quoque folio consociatae; folia pauca (4-8), disticha, subulata, 2-4 cm longa, basi 1 mm lata et equitantia, filis peripheralibus absentibus, stomatibus secus partem folii tertiam supremam dispositis, ligula minus quam 1 mm longa, triangulari, velo perfecto; megasporangia elliptico-reniformia, ca. 1 mm longa, megasporis paucis (4-20), 275-370 μm diam., triletis, demisse tuberculatis, brunneis; microsporangia elliptico-reniformia, ad 1 mm longa, microsporis multis, 26-33 μm longis, monoletis, spinulosis, brunneis.

TYPE: Heggies Rock, 3.8 mi E from Columbia Junior High School along Georgia Rte. 232 and County Road 2122, Columbia County, Georgia, 110 m elev., 33°32′30″N Lat., 82°15′05″W Long., 21 Jan 1978; solitary, dense, mat-forming population growing in a 2-4 cm thick layer of fine, siliceous soil in a S-facing pool ca. 20 m^2 and 30 cm deep containing water with a circumneutral pH, *P. M. Rury & M. Treiber 259* (NCU; isotypes B, BH, DUKE, F, GA, GH, K, KYO, MASS, MICH, NY, UNCC, US).

This unique, mat-forming population of *Isoëtes* occurs in the largest of many pools on a 90-acre granitic flatrock. This pool is unique among the pools at Heggies Rock with respect to its location, aspect, size, structure, and resultant soil and water depths. The *Isoëtes* population dominates this large pool, nearly to the exclusion of other vascular plants, by virtue of its vegetatively reproductive, mat-forming ("tegetiformans") growth habit.

The individual plants possess a slender, centrally furrowed, prostrate axis ca. 1 mm thick which exhibits bidirectional, intercalary-extension growth from the median furrow. The resultant axes are 3-35 mm long and possess both a linear phyllo- and rhizotaxis. The shoot apical meristem overlies the median furrow and develops typical *Isoëtes* leaves and sporophylls that are distichously disposed. However, unlike all other members of the *Isoëtaceae* and vascular plants in general, this shoot apex produces no cauline vascular tissue or vertical (primary) growth of the axis, and apparently has been reduced to a mere phyllogenic role. This type of distichous phyllotaxis and concomitant anatomy have been described by Paolillo (1963, p. 17) as a juvenile stage in *Isoëtes* corm development which typically persists only for the first 10-15 plastochrons of the young sporophyte.

The rhizotaxis of these plants is distinctly tristichous, a feature previously reported only for the genus *Stylites,* with two lateral rows of slender roots emerging proximal to the insertion of the leaf bases and one basal row of stout, often coiled roots which emerge proximal to the median furrow along the bottom of the axis. The roots of all specimens examined exhibit typical *Isoëtes* root anatomy but, as in *I. triquetra* and *Stylites,* are devoid of dichotomous branching. Usually three roots are produced per leaf, one from each row, and the resultant leaf-root complex becomes displaced along the axis and apparently becomes senescent as a unit. Developmentally, these three roots arise endogenously from a tracheary plexus in the vascular continuum, from which the single leaf trace departs to the associated, superadjacent leaf. This structural and developmental relationship between the roots and leaves of *I. tegetiformans* supports the contention of Liebig (1931) that the roots of *Isoëtes* are actually adventitious, as in other vascular cryptogams where roots arise in association with leaves.

The vasculature of the axes consists entirely of a sympodium of leaf and root traces which is continuous across the median furrow. The vasculature of these plants, therefore, supports the argument of both Farmer (1890) and Stokey (1909) that the vascular tissues of the *Isoëtes* stem represent a sympodium of leaf traces and that there is no true cauline portion to the stele. This sympodium, its ensheathing stem tissue, and the associated leaf-root complexes are displaced bidirectionally as a result of the sub-apical, intercalary-extension growth from the median furrow. The occurrence of a "typical" isoëtaceous cambium in the region of the median furrow suggests that the intercalary growth results from cell divisions of this cambium that are restricted to the plane of the furrow. The often contorted morphology of the prostrate axes may be the result of differential cambial activity and/or the crowded conditions of their microhabitat. Additional study of this phenomenon is clearly necessary.

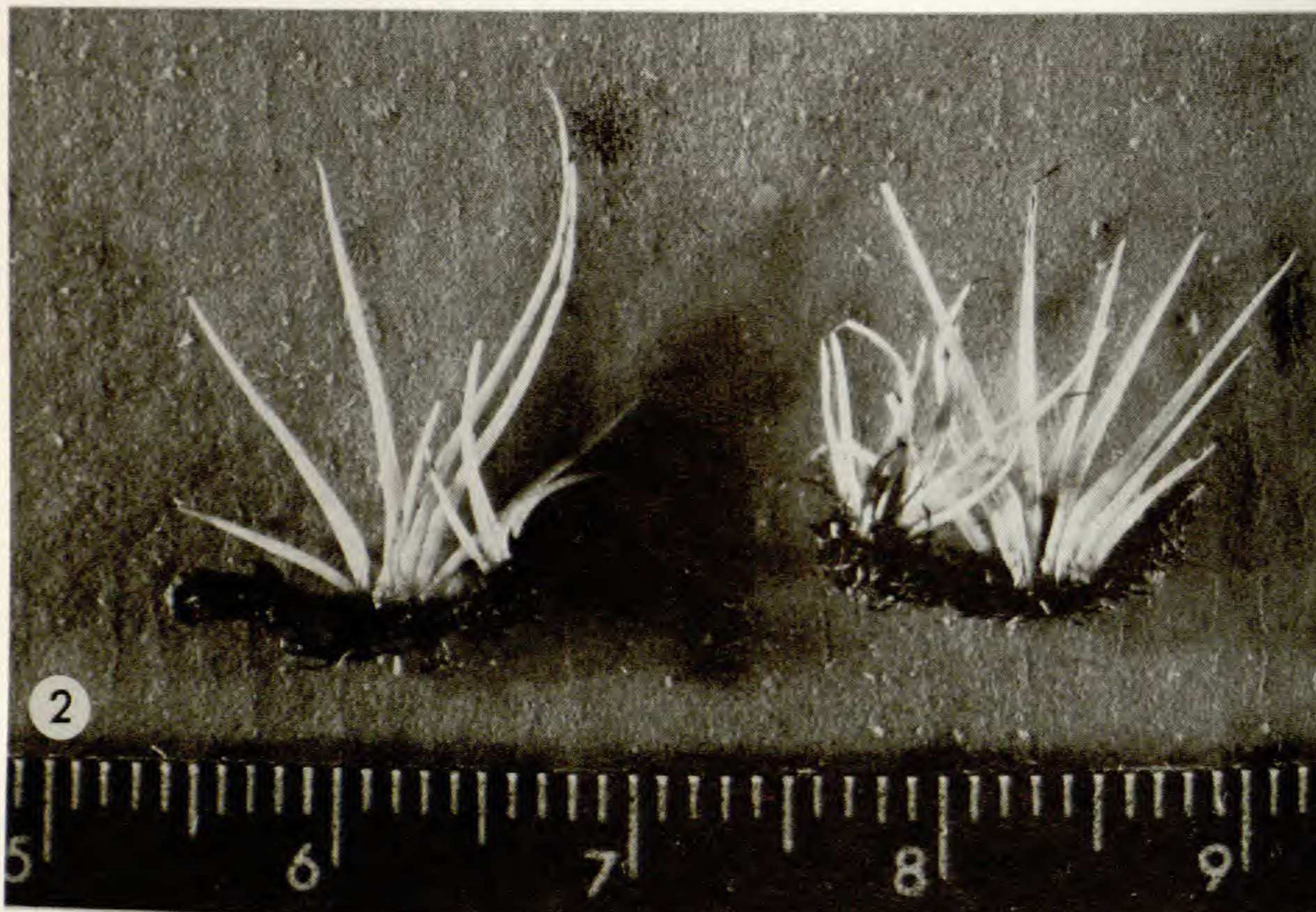


FIG. 2. Habit of *Isoëtes tegetiformans*. Double and triple plants with roots trimmed. Note the pair of distal, adventitious plantlets in the plant on the right. Scale is in centimeters.

Adventitious buds which develop into daughter plantlets are found distally on the axes at an observed minimum of 1-2 mm from the parental "leaf-producing apex." These buds arise *de novo* from the cauline storage parenchyma and form a vascular continuum that is identical to, but *non*-contiguous with, that of the parental axis. This bud formation potential is exemplified by the regeneration of seemingly dead stem fragments and by the remarkable ability of the entire population to survive repeated summer droughts and to revegetate after the water supply is replenished.

Sexual reproduction in this new species is typically isoëtaceous, and the adaxial sporangia, which do not exceed 1 mm in breadth, are completely covered by a subligular velum. The phenology of these plants apparently is seasonal, with microspores being produced in the winter-spring months and megaspores being produced in the summer-fall months. Although microsporogenesis was not observed, mature microsporangia were seen to contain numerous, brown, spinulose microspores 25-31 μm long. Megasporogenesis is typically isoëtaceous and begins with the formation of four separate megasporocytes. Four to twenty megaspores were observed per sporangium; these exhibit a low-tuberculate sculpture, are dark brown, and are 275-370 μm in diameter. The occurrence of numerous young sporelings of typical *Isoëtes-Stylites* morphology indicates that sexual reproduction is successful within the population.

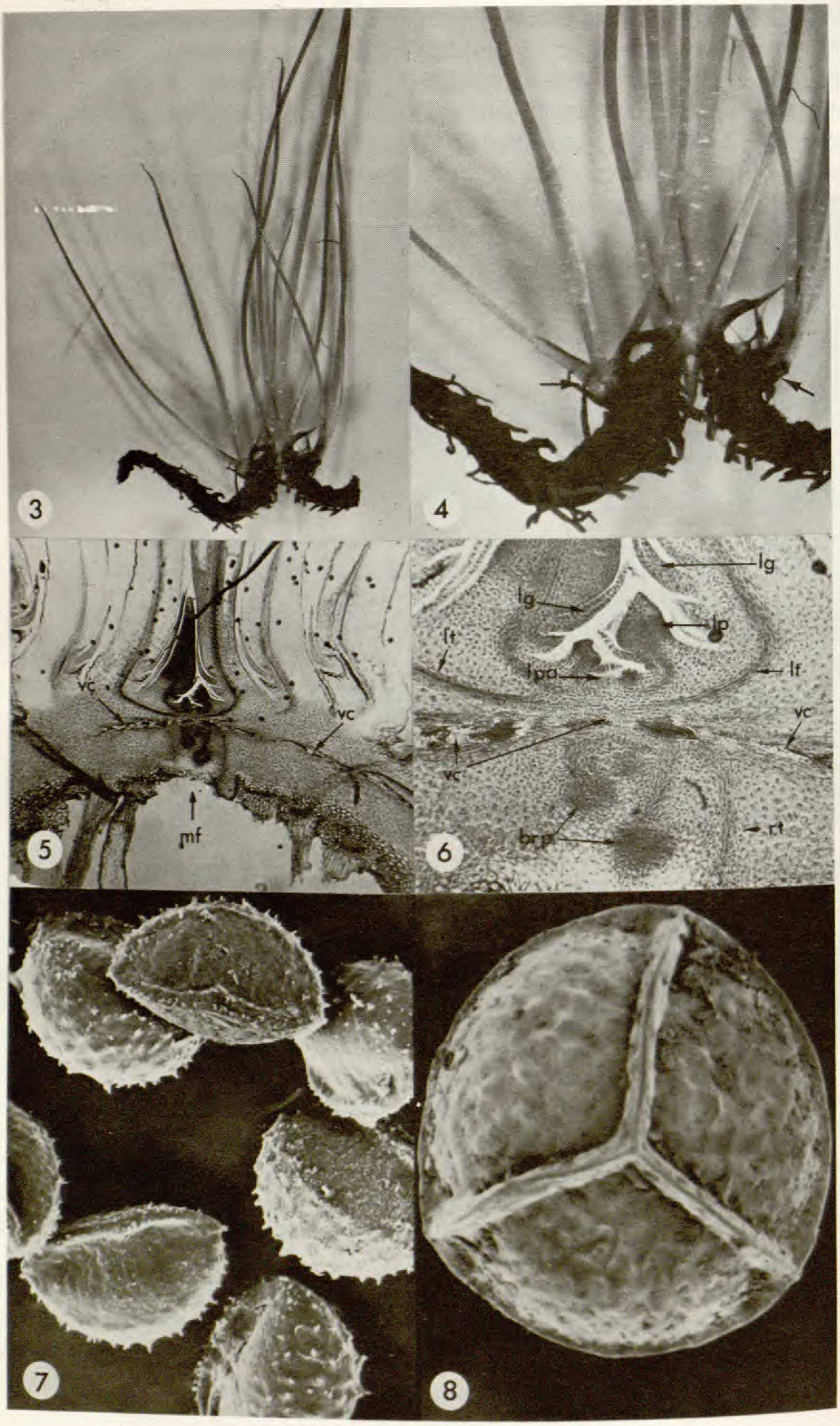
Isoëtes tegetiformans exhibits a combination of characteristics that is unique among the known species of Isoëtaceae, namely: sexual maturity in permanently distichous plants; a shoot apex which produces leaves and sporophylls only; a tristichous rhizotaxis of demonstrably adventitious roots; unbranched, frequently dimorphic roots; sympodial stem vasculature; a prostrate, intercalary growth habit; and the formation of cauline, adventitious buds.

TABLE 1. COMPARATIVE FEATURES OF *I. tegetiformans* AND *I. melanospora*.

Character	*I. tegetiformans*	*I. melanospora*
Population structure	Dense, mat-forming	Solitary, non-gregarious
Juvenile morphology and anatomy	Fixed "neoteny"	Environmentaly induced "neoteny"
Adventitious buds	Cauline	Absent
Root morphology	Non-dichotomizing, frequently dimorphic	Profusely dichotomizing, consistently isomorphic
Sporangia width	Up to 1 mm	1-2 mm
Velum coverage	Consistently complete	Complete to slight
Megaspores per sporangium	4-20	8-32 (greater for plants assignable to *I. piedmontana*)
Megaspore size	275-370 μm	350-480 μm
Megaspore sculpturing	Low tuberculate	Tuberculate to ridges
Microspore length	26-31 μm	25-30 μm
Microspore sculpturing	Spinulose	Smooth to papillate

Although unique with respect to this combination of features, this new quillwort can readily be recognized as a member of sect. *Tuberculatae* (*sensu* Pfeiffer, 1922) on the basis of its megaspore sculpture. It is interesting to note that the South American *Stylites* (2 spp.) and *I. triquetra* (the *Stylites-Isoëtes* intermediate) also are assignable to this section and are the only members of the Isoëtaceae which resemble *I. tegetiformans* in possessing non-dichotomizing roots. Within sect. *Tuberculatae, I. tegetiformans* is most similar to the members of the *I. melanospora* Engelm. complex of the southeastern United States. Unbranched specimens of *I. tegetiformans* are superficially similar to those of the incompletely described *I. melanospora* on the basis of plant size, distichous leaf arrangement, degree of velum coverage, and megaspore features. However, upon closer comparative study, a clear distinction between these two granitic endemics becomes apparent (see *Table 1*).

Isoëtes melanospora was originally described by Engelmann (1877, p. 395) from Stone Mountain, a large granitic dome in DeKalb County, Georgia. Engelmann described this Quillwort as a distichous plant with a compressed, bilobed corm inhabiting muddy pools at the summit of the granitic dome. The major reproduc-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tive features considered diagnostic for this species are sporangia completely covered by the subligular velum and black, tuberculate megaspores. Subsequent to its discovery, *I. melanospora* has been collected from several additional sites on the granitic flatrocks of the southeastern Piedmont.

In his revision of the Isoëtaceae of the southeastern United States, Reed (1965) included a species, *I. piedmontana* (Pfeiffer) Reed, which is closely related to and sympatric with *I. melanospora*. It is interesting to note in this regard that the narrow range of the granitic *I. melanospora* is included within the much broader range of *I. piedmontana*, a ubiquitous southeastern species which frequently inhabits the peripheral seepage areas and deeper soils (in pools) of these granitic outcrops. Subsequent comparative ecological and morphological study of *I. melanospora* and *I. piedmontana* has revealed the complete morphological intergradation of these two species (Matthews & Murdy, 1969). Furthermore, these authors uncovered a direct correlation between microhabitat features and the observed morphological intergradation of the populations investigated. Within a single population, they discovered that the smaller, distichous *I. melanospora* individuals are restricted to the shallower soils, whereas the larger, spiral-leaved ("typical") specimens of *I. piedmontana* consistently inhabit the areas with greater soil depths. These authors suggested that introgression of these two sympatric species might be responsible for their morphological intergradation. They apparently did not consider the possibility that these two "species" might actually represent different ontogenetic phases of the same species.

The neglect of developmental evidence in isoëtaceous taxonomy has been acknowledged by Reed (1965), who stated that "no attempt has been made to collect any one species in various phases of its growth from the same colony." I have observed both spiral and distichous individuals that are clearly assignable to *I. melanospora* (*sensu* Engelmann, 1877) within single populations at Stone Mountain and at Mt. Arabia, both in DeKalb County, Georgia. Distichous specimens were collected from both localities for comparative, uniform-environment growth studies in the laboratory. In 4-6 weeks, all of the distichous specimens from Stone Mountain and a majority of those from Mt. Arabia increased in stature and attained a spiral phyllotaxis characteristic of *I. piedmontana* and all other "typical," sexually mature Isoëtaceae. These observations, along with those of Matthews & Murdy (1969), strongly suggest that the distichous, juvenile form (*sensu* Paolillo, 1963) of *I. melanospora* merely represents an

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FIGS. 3-8. Morphology and anatomy of *Isoëtes tegetiformans*. FIG. 3. Triple, root-trimmed plant, following one year of "optimal" indoor cultivation, with two distal, adventitious plantlets, × 1.4. FIG. 4. Same as *Fig. 3*, with arrows indicating the daughter plantlets, × 3. FIG. 5. Median longitudinal section of an entire plant, at right angles to the median furrow (mf). Note the distichous phyllotaxis and the vascular continuum (vc), × 6. FIG. 6. Detail from *Fig. 5*. Note the leaf producing apex (lpa), leaf primordium (lp), ligule (lg), and the primordia of basal roots (brp). The leaf traces (lt) and root traces (lg) are components of the vascular continuum (vc), × 15. FIG. 7. Scanning electron micrograph of several monolete, spinulose microspores, × 700. FIG. 8. Scanning electron micrograph of a trilete, low-tuberculate megaspore, × 87.

arrested (neotenic) stage in the development of plants assignable to *I. piedmontana.* Although the present evidence seems convincing, further comparative biological studies of additional populations of these two "species" are desirable in order to confirm their synonymization. Nevertheless, it can be concluded that *I. melanospora* is not a strictly distichous species, as originally described by Engelmann (1877), and thus is in need of redefinition.

Having clarified reasonably well the morphological nature of *I. melanospora* and *I. piedmontana,* a clear distinction between *I. tegetiformans* and *I. melanospora sensu lato* can be made. *Isoëtes tegetiformans* resembles the distichous phase of *I. melanospora* with respect to plant size, leaf arrangement, and reproductive features. However, *I. tegetiformans* can be distinguished easily on the basis of its dense population structure; growth habit, stem morphology and anatomy, permanent distichy, unbranched, often dimorphic roots, and cauline adventitious buds. A comparison of the characteristics of *I. tegetiformans* and *I. melanospora* is presented in *Table 1.*

It is evident that the distichous, prostrate habit shared by these two granitic quillworts is merely the result of a neotenic convergence in form that is temporary in *I. melanospora* but permanent in *I. tegetiformans.* Indoor cultivation of the latter species for more than 18 months under the same growing conditions experienced by specimens of *I. melanospora* resulted in no significant morphological changes. This suggests that the neotenic form of *I. tegetiformans* is an immutable, species-specific characteristic, whereas a similar neotenic phenomenon in *I. melanospora* merely results from microhabitat influence upon the stature and correlative degree of pre-sexual morphological development of the individuals. In addition to being a fixed neotenic form, *I. tegetiformans* is also very distinct from *I. melanospora* (and all other North American species of *Isoëtes*) in having non-dichotomizing, frequently dimorphic roots and in forming numerous cauline, adventitious buds (plantlets). Beyond such general considerations, however, the precise nature of the relationship between *I. tegetiformans* and *I. melanospora* is enigmatic, and probably shall remain so until a thorough systematic study and taxonomic revision of the entire *I. melanospora* complex is completed.

The factors causing the unique morphology of this plant are presently conjectural and require further investigation. However, Lammers (1950) revealed that individuals of *I. melanospora* subjected to full sunlight at ca. 10,000 ft-c exhibit a photosynthetic rate nearly twice that of their dark respiration rate. If the photosynthetic response curve and relative rate of dark respiration are comparable for *I. tegetiformans,* then the prolific growth habit of this species is easily understood in terms of its physiology and microhabitat. The pool it inhabits is south-facing, sheltered on the north flank, and has a maximum soil and water depth that apparently is maintained by a natural, south-facing spillway from the pool. Throughout the evolutionary development of the species, this spillway may have prevented the accumulation of soil within the pool to such a degree that soil depth limited the potential stature of the plants. The long-term effect of such restrictions on plant stature, along with a potential optimal photosynthetic efficiency, may be responsible for the unique morphology and prolific growth habit of this Merlin's-grass.

Therefore, this spreading, carpet-forming species might best be regarded, evolutionarily, as an *Isoëtes* which "grew-out" like a grass instead of "growing-up" like a Quillwort.

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I would like to thank Dr. Albert E. Radford (Univ. of North Carolina, Chapel Hill) for taking me and others to Heggies Rock, the site of the present discovery, and for his diligent personal efforts to establish this outstanding granitic flatrock as a "national natural landmark area." I also wish to express my deep appreciation and gratitude to Dr. David W. Bierhorst (Univ. of Massachusetts), Amherst) for his encouragement, technical assistance, and consultation during the course of this study, and to Dr. Warren H. Wagner (Univ. of Michigan, Ann Arbor) for his encouragement and advice. Many thanks are also extended to Dr. William C. Dickison (Univ. of North Carolina, Chapel Hill) for his technical assistance and for reviewing the manuscript and to Dr. Patricia G. Gensel (Univ. of North Carolina, Chapel Hill) for her assistance in scanning electron microscopy and for her critical evaluation of the manuscript. I would also like to express my gratitude to Dr. William J. Dress (Bailey Hortorium, Cornell University) for his assistance in preparing the Latin species description and to Dr. Timothy C. Plowman (Botanical Museum, Harvard University) for his helpful comments.

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REVIEW

"TENTAMEN PTERIDOPHYTORUM GENERA IN TAXONOMICUM ORDINEM REDIGENDI," by R. E. G. Pichi Sermolli, Webbia **31:** 313-512. 1977.—Professor Pichi Sermolli has written a most detailed and exhaustive treatment of fern classification down to the level of genus. His treatment is illustrated with a table of families and tree-like diagrams of the genera or groups of genera within each family, and includes a conspectus of the families and genera with generic numbers allowing for intercalation of additional genera, an index of the genera and their synonyms, and discussions of the genera and their characteristics.

In contrast to most linear arrangements of genera proposed in the past, Pichi Sermolli's treats all the genera of a single line of evolution from primitive to advanced before passing on to another line of evolution. In my opinion, this is a more natural and satisfactory method than is treating first all primitive genera and then all advanced ones, regardless of which of several phyletic lines they belong to.

His classification groups 443 genera of living pteridophyta into 64 families—both record high numbers. Many of the genera I consider subgenera at best. Judging by the lengthy discussion of the genera, Pichi Sermolli gives more weight to certain differences in morphology than do most authors; he is a self-admitted splitter.

There is one good reason for such splitting in proposing a classification: it forces users to consider the differences between finely split genera which otherwise might be ignored. The disadvantage is that in using one level of classification rather than two (genus and subgenus), Pichi Sermolli's classification contains less information about relationships of genera within his families. Fortunately, his tree-like diagrams convey this information, although his conspectus and any herbarium arrangement based on it would not. Whether one adopts finely split genera or more comprehensive ones is to some extent a matter of personal preference or need, but either way Pichi Sermolli's work will be very useful for a long time to come.—*D.B.L.*